ONTOGENY OF THE TRILOBITE *PELTURA SCARABAEOIDES* FROM UPPER CAMBRIAN, DENMARK

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ABSTRACT. Poulsen's original material of the developmental stages of *Peltura scarabaeoides* is redescribed. It includes protaspides of length 0·4 mm. and cranidia or cephala up to a length of 1·6 mm. The protaspid glabella is elliptical in outline, widest at the mid-length, and divided into five rings. In meraspid cephala of length greater than 1 mm. the glabella is widest across the occipital ring and glabellar furrows are lateral. The outline of the anterior cephalic margin changes from forwardly concave to forwardly convex. In a cephalon of length 1 mm. (including occipital spine) the posterior branch of the facial suture crosses the cephalic border immediately outside the base of the fixigenal spine. In a smaller cranidium and the protaspis the exact course cannot be seen, but it may be similar. The fixed cheeks become narrower relative to the occipital ring as size increases, in contrast to their development in other olenids. Fixigenal and median occipital spines are present in a cranidium of length 1·3 mm., but not in larger cranidia. The ontogeny of the cephalon of *P. scarabaeoides* is, among olenids, most like that of *Leptoplastides salteri*.

It was claimed by Poulsen that a considerable migration of the posterior branch of the suture occurred in small cephala of *P. scarabaeoides*. Such a migration cannot be demonstrated, and theoretical deductions based in part on this claim are now open to doubt.

INTRODUCTION

THE view expressed by Poulsen (1927, pp. 330–1) that opisthoparian genera pass through a proparian stage in their ontogeny, was to a large extent based on his investigation (Poulsen 1923, pp. 58–59, 83, fig. 22; 1927, p. 330) of developmental stages of *Peltura scarabaeoides*. In the smallest meraspid head-shield (Pl. 38, fig. 9) the posterior branch of the suture is portrayed by Poulsen as running out from the eye lobe in a curve concave forwards, and crossing the lateral cephalic border at a point in advance of the mid-point of the cephalic length, opposite the second glabellar ring furrow from the anterior. In the next largest cephalon (Pl. 38, fig. 12) the posterior branch is portrayed as running in a curve convex outwards, and crossing the lateral border a short distance in front of the base of the fixigenal spine. In an holaspid cranidium (Pl. 38, fig. 18) the posterior branch crosses the extremity of the posterior cephalic border. Thus the change from a proparian to an opisthoparian sutural condition during ontogeny implied a considerable migration of the point where the posterior branch crosses over the cephalic border and on to the doublure.

The award of a Guggenheim Memorial Fellowship enabled me to visit Copenhagen in May 1957, and Professor Chr. Poulsen afforded me every facility in studying and photographing the original material of *P. scarabaeoides*. I am indebted to Professor Poulsen for his kindness in urging me to publish this redescription. I consider that the smallest post-protaspid developmental stage is a cranidium. The exact course the posterior branch follows cannot be determined. The next largest specimen is a cephalon, and the posterior branch of the suture crosses the border immediately in front of the fixigenal spine, a sutural condition that is usually termed proparian. The considerable change in position of the course followed by the posterior branch of the suture implied in Poulsen's earlier description cannot be demonstrated. It is my opinion that, to

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describe the early developmental stages of *P. scarabaeoides* as proparian may be misleading if by 'proparian' the impression is conveyed that the posterior branch of the suture crosses the lateral cephalic border far in advance of the genal angle. I have discussed elsewhere the ontogeny of other species supposed to show a sutural history like that formerly claimed for *P. scarabaeoides*, marshalled evidence that leads me to believe that they may not go through such a history, and considered the implications of these discoveries (Whittington 1957*a*, *b*). In brief, if the cephala of early meraspides of *P. scarabaeoides* and like trilobites are termed 'proparian', it is only, so far as we know, by virtue of the posterior branch crossing the border immediately in advance of the fixigenal spine. Bearing in mind other morphological characters of these meraspides, it does not seem probable to me that by arrested development they could have given rise to post-Cambrian proparian trilobites.

The terminology used here follows that of earlier papers (e.g. Whittington 1957*a*, fig. 1) and employs the abbreviations sag. (sagittal, in the median line), exs. (exsagittal, parallel to the median line), and tr. (transverse, at right angles to the median line) to define the particular direction under discussion. The new measurements have been made by Professor Poulsen.

Family OLENIDAE Burmeister 1843
Subfamily PELTURINAE Hawle and Corda 1847
Peltura scarabaeoides (Wahlenberg 1821)

Plate 38, figs. 1–18

Material. The originals of Poulsen 1923, pp. 58–59, 83, figs. 22*a–c*, are preserved in four small pieces of black, bituminous limestone (stinkstone or anthraconite) containing abundant parts of trilobite exoskeletons. They are deposited in the Museum of the Mineralogical-Geological Institute, University of Copenhagen, and numbered 1987 (two pieces), 1988 and 1989.

Geological Horizon and Locality. Upper Cambrian Olenid Series, *P. scarabaeoides* zone Vc (Henningsmoen 1957, pp. 237–9, 300) from a well excavation at Lille Duegaard, Aaker parish, island of Bornholm, Denmark. Collected by K. A. Grönwall, Professor Poulsen informs me that the locality is no longer accessible.

Description. Besides the originals of Poulsen (Pl. 38, figs. 1–3, 5, 6), which are 0·42 mm. in length (sag.), there is another protaspis on each of the pieces numbered 1988 and 1989. All four specimens are about the same size, subcircular in outline, strongly convex. Axis divided by furrows into six rings, the anterior furrow shallower than those following. Axis widest across the second ring from the anterior or across the furrow defining this ring posteriorly, tapering progressively anteriorly and posteriorly from greatest width. Frontal lobe and following three rings of about equal length (sag.), strongly convex, next ring posteriorly (occipital) shorter (sag.) but as convex, posterior ring short, much less convex, and situated on steeply-sloping posterior part of shield. Axial furrow well defined, anterior pit shallow. Pleural regions convex, sloping steeply laterally and most steeply posteriorly beside tip of axis. A convex border, defined by a border furrow, bounds the pleural region laterally, and merges postero-laterally into the base of the short, outward and downwardly directed fixigenal spine. Antero-laterally the border becomes wider and less well defined, and is bounded anteriorly by a faint furrow which

runs from the anterior pit outward and forward to the margin. In front of this furrow is the tiny anterior border, which narrows and disappears inwards as it approaches the margin of the frontal axial lobe. The posterior margin of the shield, between the bases of the fixigenal spines, is partly concealed and thus ill defined in all the specimens. The outline may be transverse or gently convex posteriorly. In one specimen (Pl. 38, figs. 5, 6) what appears to be a posterior border furrow runs outward (and slightly backward) from opposite the occipital ring furrow to merge distally with the lateral border furrow. Behind this furrow is a faint, low posterior border which runs out opposite the occipital ring and into the base of the fixigenal spine. The protopygidial part of the protaspis is thus short (sag. and exs.) and narrow.

The next largest specimens are of sagittal length, *c.* 0·5 mm. (Pl. 38, figs. 8, 9, the original of fig. 9 measuring 0·54 mm.), there being a third example, showing the short median occipital spine on the smaller piece numbered 1987. Glabella subcylindrical, divided into five rings by furrows which are progressively deeper posteriorly, and only slightly wider across the median than the frontal or occipital ring. Latter ring shorter (sag.) than those in front, which are about equal in length. Deep anterior pit at extremity of deep axial furrow. Anterior cephalic border narrowest in median line, widening progressively distally to give a forwardly concave outline to the anterior margin of the shield. Anterior border furrow runs out from anterior pit. Convex pleural region with lateral and posterior borders well defined by furrows, the borders widening toward the base of the fixigenal spine. This spine is long, directed slightly outward and horizontally (not downwardly as in the protaspis). Palpebral lobe is wider and higher than the adjacent part of the lateral border, clearly defined on the inner side by a palpebral furrow, and continuous at the anterior extremity with a low eye ridge. This latter runs directly inward to reach the axial furrow immediately behind the anterior pit. Surface of pleural region coarsely granulate.

The next largest specimen is of a cephalon with the free cheeks only slightly displaced

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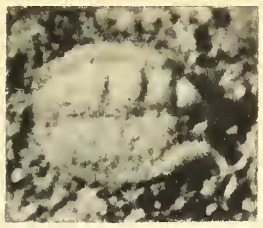
EXPLANATION OF PLATE 38

Fig. 1–18. *Peltura scarabaeoides* (Wahlenberg), Upper Cambrian Olenid Series, Bornholm, Denmark. Catalogue numbers of the Museum of the Mineralogical-Geological Institute, University of Copenhagen. 1–3, protaspis, latero-dorsal, dorsal, postero-dorsal views, no. 1987, original of Poulsen 1923, fig. 22*a*, left, ×40. 4, protaspis, partial reconstruction in dorsal view, *c.* ×54. ab = anterior border, ap = anterior pit, fx = fixigenal spine, lb = lateral border of pleural region, or = occipital ring, pb = posterior border of cephalon, pl = palpebral lobe. 5, 6, protaspis, postero-dorsal and dorsal views, no. 1987, original of Poulsen 1923, fig. 22*a*, right, ×40. 7, protaspis, reconstruction in latero-dorsal view, *c.* ×54. *a* = supposed point where anterior branch of suture crosses margin of anterior border, *b* = supposed point where posterior branch of suture crosses margin of lateral border. Other letters as in fig. 4. Dashed line indicates position of margin of hypothetical free cheek. 8, incomplete cranidium, dorsal view, no. 1987, ×30. 9, cranidium, dorsal view, no. 1988, original of Poulsen 1923, fig. 22*b*, left, ×30. 10, cranidium, dorsal view, based on original of fig. 9, *c.* ×40. abs = anterior branch of suture, er = eye ridge, pbs = supposed course of posterior branch of suture, sr = sutural ridge. Other letters as in fig. 4. Dashed line indicates supposed position of margin of free cheek. 11, 12, cephalon, latero-dorsal and dorsal views, no. 1988, original of Poulsen 1923, fig. 22*b*, right, ×30. 13, cephalon, dorsal view, based on original of fig. 12, *c.* ×28. Letters as in figs. 4, 10. 14, external mould of incomplete cranidium, oblique view, no. 1989, ×15. 15, 18, cranidium, anterior and dorsal views, no. 1989, original of Poulsen 1923, fig. 22*c*, ×15. 16, incomplete free cheek, oblique view, no. 1989, ×15. 17, incomplete free cheek, oblique view, no. 1988, ×15.



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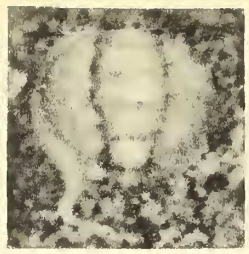

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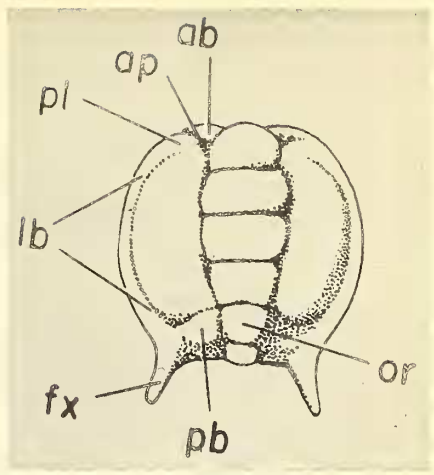

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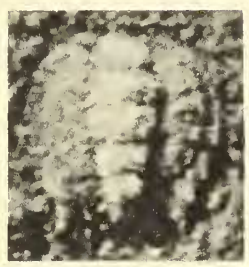

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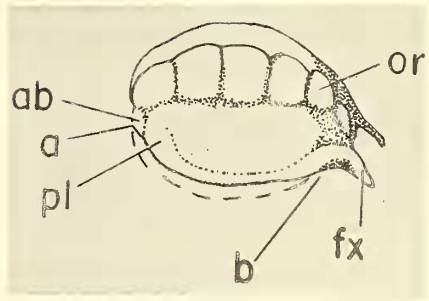

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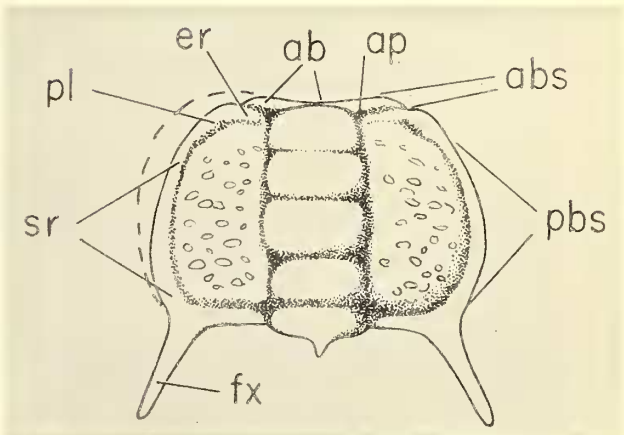

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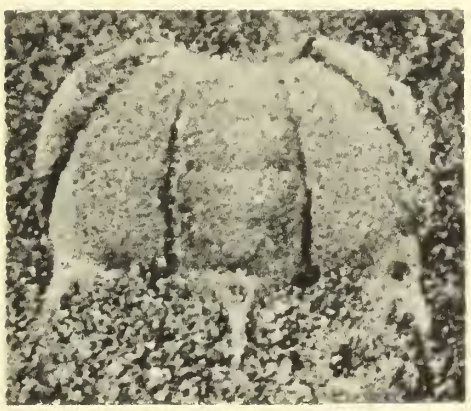

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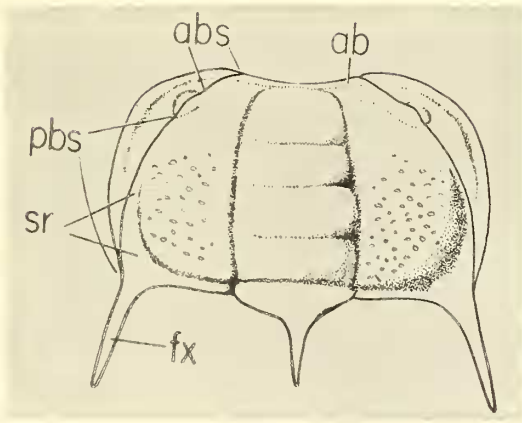

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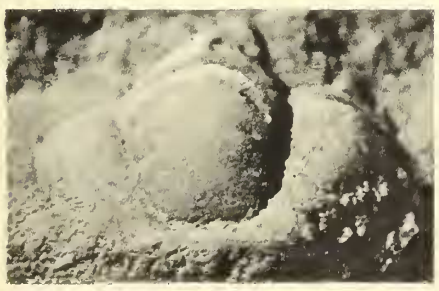

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WHITTINGTON, *Peltura scarabaeoides*

(Pl. 38, figs. 11, 12). Length (sag.), including median occipital spine, 1·02 mm. Glabella divided by shallow furrows into five rings, occipital furrow deeper than those in front and occipital ring shorter (sag.) than the rings anterior to it. Glabella widest across median ring, tapering markedly to frontal lobe and only slightly to occipital ring. Anterior pit faint. Anterior border narrowest at mid-line, widening and curving forward distally to give concave anterior marginal outline to cephalon. Long fixigenal and median occipital spines. A low broad ridge runs forward from the base of the fixigenal spine, following the course of the posterior branch of the suture, and dies out at about the mid-length of the fixed cheek. Palpebral lobe and eye ridge low and ill defined. Free cheek widest (tr.) opposite eye lobe, low border defined by shallow furrow. Course of anterior and posterior branch of suture clearly shown by displacement of free cheeks, and posterior branch curves back to cross the margin of the pleural region at the outer edge of the base of the fixigenal spine.

Larger specimens include cranidia of length 1·33 mm. (Pl. 38, fig. 14) and 1·56 mm. (Pl. 38, figs. 15, 18) and incomplete free cheeks (Pl. 38, figs. 16, 17). The smaller of these cranidia has the glabella crossed only by the occipital furrow (across which it is widest), first and second lateral glabellar furrows extending diagonally inward about one-third the width, and faint third furrows. The anterior marginal outline of the cranidium is convex forward, there is a short median occipital spine and a longer fixigenal. The larger cranidium is of the same general form, the third glabellar furrow extremely faint, palpebral lobe opposite this furrow, and eye ridge faint. Median occipital tubercle and short median spine immediately behind it. Fixigenal spine absent.

The largest cranidium and free cheek in the Danish material is one-third or less the size of specimens of the typical sub-species illustrated by Henningsmoen (1957, pl. 25, fig. 13; pl. 26, fig. 1). Comparisons with these figures suggest that, as size increases, the glabella assumes a sub-square rather than sub-conical outline, and becomes relatively wider. The free cheek changes in outline so that the postero-lateral curvature of the margin is greater, and the maximum width farther back.

Discussion. My interpretation of the protaspis and two succeeding stages is shown in Pl. 38, figs. 4, 7, 10, 13. Facial sutures can first be observed unequivocally in the small cephalon (Pl. 38, figs. 11, 12). A low ridge runs forward from the base of the fixigenal spine along the border of the cranidium and dies out at about half the length. At least the anterior part of this ridge may be a structure distinct from the cephalic border (best preserved on the right free cheek), and is so shown in Pl. 38, fig. 13. The ridge is termed the sutural ridge because it runs beside the suture. In larger specimens the sutural ridge is extremely faint (Pl. 38, fig. 14) or cannot be distinguished (Pl. 38, fig. 18). In the next smallest specimens (Pl. 38, figs. 8, 9) the sutural ridge is well defined and extends forward to form a continuous structure with the eye lobe (and hence at least the anterior part of the sutural ridge may be a structure distinct from the lateral cephalic border, which in later developmental stages may be seen to run outside the eye lobe). It appears to me that this specimen is a cranidium, bounded laterally by the two branches of the suture. How far back the posterior branch extended before crossing over the margin of the cephalon and on to the doublure is a matter that cannot be decided from the available material. I have suggested a course analogous to that in the next largest specimen, and the possible outline of the free cheek by a dashed line.

In the protaspis (Pl. 38, figs. 4, 7) I suggest that the slightly wider, antero-lateral part of the border is the palpebral lobe, and that the remainder of the lateral border represents the sutural ridge of larger specimens. If sutures were developed, as they are in other small protaspides (Whittington 1957*a*), they may have followed a course along the outermost parts of the pleural regions. The shape of the distal part of the anterior border suggests that there may have been a suture which ran from the point *a* in Pl. 38, fig. 7, across the anterior border, bounded the palpebral lobe, and extended an unknown distance back along the lateral pleural border (= sutural ridge of larger specimens). In lateral view (Pl. 38, fig. 1) this border is wide for a short distance in front of the fixigenal spine, then narrows rather abruptly. I suggest that this change in width is determined by the suture extending back on the dorsal side to the point *b* in Pl. 38, fig. 7, before it crosses on to the doublure. I have also indicated an outline of the hypothetical free cheek consistent with these views.

Authors are agreed that the sutural condition of holaspid *Peltura* should be termed 'opisthoparian'. In larger specimens than those illustrated here (e.g. Henningsmoen 1957, pl. 2, fig. 1) the outline of the postero-lateral part of the free cheek is strongly angular, giving a decisively 'opisthoparian' appearance to the cephalon. It is also prevailing practice to term an olenid cephalon 'proparian' if a fixigenal spine is present and the suture crosses the margin just outside the base of this spine (e.g. *Saltaspis* in Henningsmoen 1957, p. 244, pl. 2, fig. 11; Harrington and Leanza 1957, p. 93, fig. 31). Thus the original of the present Pl. 38, fig. 12 may likewise be termed 'proparian', and one may continue to say that *P. scarabaeoides* exhibits the proparian condition in early developmental stages. However, the point where the posterior branch of the suture crosses the cephalic border in the original of Pl. 38, fig. 12 is similarly situated to that in small cranidia of *Flexicalymene* (Whittington 1941, pl. 72, fig. 4)—a disputed 'proparian'—but is far posterior to that in such 'typical' proparia as phacopids or cheirurids (Whittington 1957*a*, figs. 16, 18). It appears to me that a mistaken impression may thus arise from characterizing the early stages of *P. scarabaeoides* as 'proparian'. The course followed by the posterior branch in the protaspis and earliest known meraspis remains open to conjecture, but I have surmised (Pl. 38, figs. 7, 10) that it may have been much the same as in the small cephalon (Pl. 38, fig. 12).

Among olenids the protaspid and meraspid development of *Olenus gibbosus* is known (Strand 1927; Størmer 1942), and the development from meraspid degree 1 onwards of *Leptoplastides salteri* (Raw 1925) and *Triarthrus eatoni* (Whittington 1957*a*, *b*). The protaspis of *O. gibbosus*, of the same size as that here described of *P. scarabaeoides*, has the same general form, but the outline of the glabella is strikingly different, being widest anteriorly and tapering back to the occipital ring. The pleural border (= sutural ridge) is present only postero-laterally in *O. gibbosus*, and the spines on the posterior border, possibly fixigenal, are small. Meraspid cranidia of about 0·5 mm. length of *O. gibbosus* differ principally from those of *P. scarabaeoides* in having the frontal glabellar lobe the widest, and this lobe exhibits both a short lateral furrow at the mid-length and a short median anterior furrow. The anterior cranidial margin in *O. gibbosus* is straight, and the sutural ridge and a tiny fixigenal spine are present. Cranidia of *O. gibbosus* of about 1·0 mm. length are distinguished by the presence of the pre-glabellar field, more prominent palpebral lobe and eye ridge, and absence of fixigenal spine.

Cephala of *L. salteri* of meraspid degrees 3 and 5 are of about the same size as the